

TOUGH AFRICAN MODELS AND WEAK MIMICS: NEW HORIZONS IN THE EVOLUTION OF BAD TASTE

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ABSTRACT. Mean hindwing toughness was measured experimentally and compared among three sympatric African nymphalid butterflies comprising an aposematic model, its Batesian mimic, and a palatable, non-mimetic relative of the mimic. The unpalatable model species had the toughest wings and palatable species had the weakest. Implications for assessing butterfly palatability and mimicry are discussed in light of previous work, and a wing toughness spectrum is proposed as a potential correlate of the palatability spectrum.

Additional key words: butterfly mimicry, *Amauris albimaculata*, *Pseudacraea lucretia*, *Cymothoe herminia*.

Insectivorous birds have likely influenced the evolution of butterfly coloration and behaviors by attacking and eating adult butterflies (Poulton 1902, 1908, Carpenter 1932, 1937, 1938, Wourms & Wasserman 1985). Depending on where they fall on the theoretical palatability spectrum, some butterfly species are eaten by birds, while other species are avoided (e.g., Brower 1958a, b, Turner 1984, Turner & Speed 1999). Generally distasteful butterflies minimize predation by advertising noxious qualities with conspicuous color patterns and a slow flight, while palatable ones use cryptic coloration and rapid flight to evade predators (Fisher 1958, Chai 1986, 1996, Chai & Srygley 1990, Pinheiro 1996). Still other palatable butterflies diminish predation by mimicking distasteful species. The elegance of mimicry stems from the fact that mimics may show strong phenotypic and behavioral resemblance to their models, regardless of taxonomic relatedness among the species involved (Fisher 1958, Turner 1987, Srygley 1994, Joron et al. 2001).

The evolution of warning coloration and mimicry requires differential survival of some individual butterflies following attacks and tasting by predators, and that the experience be memorable to predators (Fisher 1958). For example, the bodies of aposematic and unpalatable Danainae are well known to be more resilient to damage from bird attacks than cryptic and palatable Satyrinae (Poulton 1908, Carpenter 1942, Chai 1996, Pinheiro 1996). Here natural selection seems to have favored aposematic phenotypes that are resistant to handling by predators, and at the same time allowed for continued advertising of the unpalatable phenotypes. In sum, body toughness in butterflies appears to be correlated with unpalatability.

Recent experimental work extends our understanding of unpalatable traits in butterflies by showing that wings of aposematic African danaine and acraeinae species are significantly tougher than those of cryptic, palatable nymphalines and satyrines (DeVries 2002). The study suggested that, in addition to body resilience, relative wing toughness may be correlated

with palatability, and that the spectrum of butterfly wing toughness needs to be documented more broadly. Accordingly this report explores palatability and toughness in a different light by asking whether African models are tougher than their mimics. To do so differential wing toughness was estimated among three sympatric nymphalid butterflies that represent an unpalatable model, a Batesian mimic, and a palatable, non-mimic.

MATERIALS AND METHODS

The study was conducted from 12–25 August 2001 in western Uganda at the Kibale Forest field station that forms part of the 766 km² Kibale National Park (0°13' to 0°41'N; 30°19' to 30°32'E) adjacent to the western arm of Africa's Rift Valley. The park lies between altitudes 1110 m in the south and 1590 m in the north. Classified as a moist evergreen forest, Kibale Forest has affinities with both montane forest and mixed tropical deciduous forest. The area around the preserve is a matrix of second growth forest, small agricultural plots, associated riparian edges, and has a long history of various human activities, including long-term studies of forest primates (summarized in Struhsaker 1997).

Based on their relative abundance during the study three butterflies were selected to represent palatable or unpalatable species. The trio was formed by a model species, its Batesian mimic, and a cryptic, non-mimetic species that is closely related to the mimic. Palatability and mimetic resemblance were assessed by direct field observations on their color pattern, flight behavior, sympatry, and inference from a detailed literature (Marshall 1902, Swynnerton 1915a, b, Carpenter 1941, Brower 1984, Ackery & Vane-Wright 1984, Turner 1984, Ackery 1988, Larsen 1991). These criteria strongly suggested that *Amauris albimaculata* Butler (Danainae) is an unpalatable model for the putatively palatable Batesian mimic *Pseudacraea lucretia* Neave (Nymphalinae), and that *Cymothoe herminia* Grosse-Smith (Nymphalinae) is a palatable, non-mimetic species closely related to *P. lucretia*.

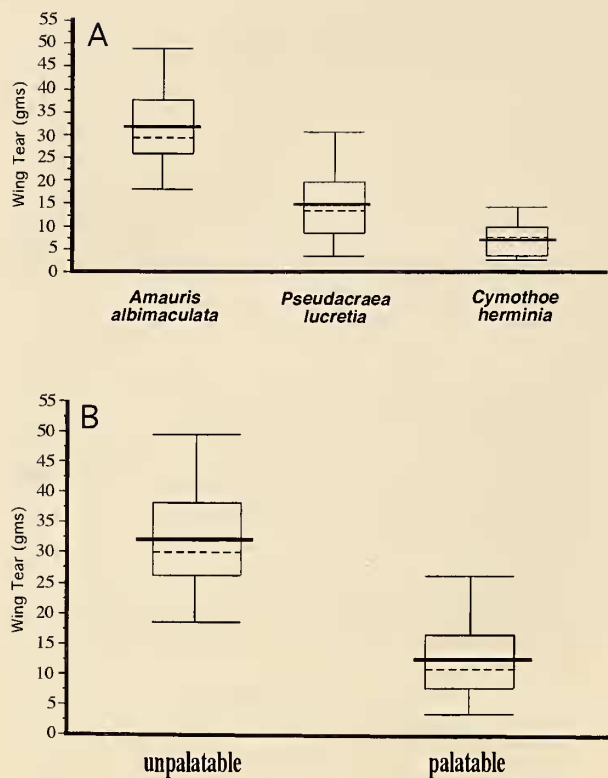


FIG. 1. Box plot comparisons of wing tear weights. Each box spans the first to third quartile and the vertical bars extend to the maximum and minimum values of the sample. Within each box the median is shown by the dashed line, and the mean by the solid line. **A**, Comparison of wing tear weights for species. Sample sizes are as follows: *Amauris albimaculata* ($N = 10$), *Pseudacraea lucretia* ($N = 23$) and *Cymothoe herminia* ($N = 14$). **B**, Comparison of wing tear weights of all species grouped by palatable and unpalatable categories.

As done in DeVries (2002) an experimental bird-bill was fashioned using a small metal electrical clip with a small plastic weighing dish tied with thread opposite the clip's jaws (hereafter, the clip assembly). A butterfly was killed by a pinch to the thorax, then immediately secured in the jaws of a wooden clothes peg attached to a rigid wire suspended from the center post below the legs of a photographic tripod. All individuals were secured with the wings closed in a natural resting position such that the clothes peg gripped all four wings. The clip assembly was then carefully attached to the hindwing distal margins of the butterfly such that the jaws gripped the wings between veins Cu_1 and $2A$. This position closely approximates that of beak marks made by birds attacking resting butterflies (e.g., Carpenter 1932, 1937, 1938, 1941, Collenette & Talbot, 1928, PJD pers. obs.). The tripod center post was then raised slowly until the weighing dish was freely suspended about 20 mm above a receptacle. Once suspended, tiny ball bearings were slowly added to the dish until the clip as-

sembly tore free of the wing, falling into the receptacle below. The tear in the wing closely simulated wing damage inflicted by birds in the wild (DeVries 2002). The clip assembly and ball bearing weights were then weighed to the nearest 0.001 g on a model PB53 Mettler-Toledo™ electronic balance. This weight established the force necessary to tear the clip assembly free of the hindwings, and provided a measure of relative wing toughness for each individual specimen.

Individual butterflies that had any wing damage or faded wing-patterns due to old age were not used. This avoided potential effects of wing condition on measures of wing-length or relative wing toughness. To estimate body size by species the distance from base to apex of one wing was measured with dial calipers to the nearest 0.1 mm for all individual specimens.

Differences in wing tear weights and forewing lengths among species were evaluated using a one-way ANOVA. The potential relationship between tear weight and wing length was tested for each species using linear regression. Significance levels for mean wing tear-weight and length in paired comparisons were adjusted for non-independence using the sequential Bonferroni-Dunn method (Rice 1989). Wing tear weights were evaluated using a one-way ANOVA for model, mimic and non-mimetic species, and for pooled palatable and unpalatable species.

RESULTS

Mean wing tear weights differed significantly among the individual species ($F = 35.523$, $p < 0.001$, $df = 2$), where *A. albimaculata* had the toughest wings, *P. lucretia* less tough wings, and *C. herminia* had the weakest wings (Fig. 1A). Comparison of species pairs showed significant wing tear weight differences between species (Table 1A). As a group, unpalatable butterflies had significantly higher wing tear weights than palatable ones (Fig. 1A, B) ($F = 51.135$, $p < 0.0001$, $df = 1$). Tear-weights also differed among species pairs representing model, mimic and non-mimetic butterflies (Table 1A).

Wing lengths differed among species ($F = 5.562$, $p = 0.007$, $df = 2$), between species (Table 1B), and unpalatable butterflies had greater mean wing lengths than palatable ones ($F = 5.084$, $p = 0.029$, $df = 1$). Although the largest species, *A. albimaculata*, had the highest tear weight (Fig. 1A, Table 1), linear regression showed no significant relationship between wing-length and tear weight among species; all probability values were between 0.8580 and 0.4599, and all R^2 values were between 0.004 and 0.044.

DISCUSSION

Butterflies are not discretely palatable or noxious to predators, but rather they encompass a theoretical palatability spectrum (reviewed in Turner 1984, 1987). The palatability spectrum refers to the relative tastiness of potential prey that, depending on the species, is potentially distributed from delicious to positively noxious for particular predators. For example, groups of closely related butterflies (e.g., Danainae, Heliconiinae) may include species that range from those eaten by birds to those that are always rejected because they possess a nasty taste (Turner 1984, Ritland 1991, Chai 1996, Srygley 1994, Pinheiro 1996). The concept of a palatability spectrum has challenged the traditional separation of Batesian and Müllerian mimicry in butterflies, and forces us to consider these discrete mimetic categories in a new light (Rothschild 1971, 1981, Huheey 1988, Turner 1984, 1987, Speed & Turner 1999, Turner & Speed 2001, Joron et al. 2001, Mallet 2001).

Empirical and theoretical work suggests that unpalatable butterflies should evolve physical attributes making them resistant to handling by predators (e.g., Poulton 1908, Carpenter 1938, 1941, 1942, Fisher 1958). By estimating the force necessary to tear wings this report corroborates the hypothesis that wing toughness may be a correlate of unpalatability in butterflies (DeVries 2002). Here the aposematic model (*A. albimaculata*) had significantly tougher wings than its putative Batesian mimic (*P. lucretia*) and a palatable non-mimic (*C. herminia*), and that the mimic had significantly tougher wings than its non-mimetic relative (Fig. 1, Table 1). If predators use wing toughness to help assess butterfly palatability, these observations support the idea that, in addition to sharing behaviors and color patterns with their models, some Batesian mimics may be to some degree unpalatable (e.g., Carpenter & Ford 1933, Rothschild 1971, 1981, Turner 1984, Ritland 1991). Using wing toughness as a metric, the cryptic species, *C. herminia*, would be the most palatable of the trio examined here. Obviously a larger study comparing many aposematic, mimetic and cryptic butterfly species is needed to help reveal evolutionary correlates and phylogenetic patterns of wing toughness. Nevertheless, in concert with other work (Carpenter 1941, DeVries 2002), the present investigation supports the concept of a wing toughness spectrum that has evolved in parallel with the palatability spectrum.

It seems likely that differential wing toughness is correlated with the category and location of damage marks left by predators on the wings of palatable and

unpalatable nymphalid butterflies. Because their wings are tougher, beak marks (impressions on the wings) should be observed more frequently among unpalatable species whereas wing tears (areas removed from the wing) should be observed with a higher frequency among palatable species than unpalatable ones. This indeed seems to be the case in specimens recovered from nature (e.g., Carpenter 1932, 1937, 1938, 1941, Collenette & Talbot, 1928), and it would be useful to compare predator damage among species that fall along a wing toughness spectrum. Bird attacks are most frequently directed to the hindwing in resting butterflies (Carpenter 1944), and in palatable species distinct patterns at the hindwing margin may function as targets that divert predator attacks away from vital body areas (Blest 1957; Wourms & Wasserman 1985); the attacked butterfly may escape leaving the predator with only a piece of wing. Thus, we might expect to find the location of wing tears to be biased toward the target areas (e.g., eyespots of Satyrinae) in palatable species, and greater variance in location of beak marks in unpalatable species without target areas. As pointed to previously (DeVries 2002), differential wing toughness raises the question as to whether hindwing target areas in palatable species are weaker than the wing areas surrounding them.

Our understanding of butterfly mimicry has depended on continued reassessment of theory in light of empirical observation (e.g., Carpenter & Ford 1933, Fisher 1958, Rothschild 1971, 1981, Benson 1977, Owen 1971, Cuthill & Bennett 1993, DeVries et al. 1999, Joron et al. 1999, Speed & Turner 1999, Turner & Speed 2001). This and a previous study (DeVries 2002) establish a motive for a comparative study on differential wing toughness as an evolutionary corre-

TABLE 1. **A**, Wing tear differences among species pairs. **B**, Wing length differences among species pairs. Bonferroni/Dunn comparisons are significant at $p \leq 0.0167$. Abbreviations: * = significant, n.s. = not significant.

A				
Comparison	Mean wing tear	Critical difference	p	Significance
<i>albimaculata</i> × <i>herminia</i>	24.433	7.299	<0.0001	*
<i>albimaculata</i> × <i>lucretia</i>	16.897	6.678	<0.0001	*
<i>herminia</i> × <i>lucretia</i>	-7.536	5.976	<0.0030	*
B				
Comparison	Mean wing length	Critical difference	p	Significance
<i>albimaculata</i> × <i>herminia</i>	3.327	2.562	0.0023	*
<i>albimaculata</i> × <i>lucretia</i>	1.346	2.343	0.1599	n.s.
<i>herminia</i> × <i>lucretia</i>	-1.981	2.097	0.233	n.s.

late among many palatable and distasteful butterflies. They also suggest new ways of assessing the palatability spectrum among butterflies that have been traditionally considered palatable mimics. Finally, the methods used here provide a means for asking whether model butterflies are tougher than mimics, and if non-mimic butterflies are the weakest of all. By exploring the parallel between the palatability spectrum and wing toughness we may potentially open new horizons in the evolution of bad taste.

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